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Behavior of the Amazon Dolphin, *Inia geoffrensis*
(Blainville), in Captivity

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(Plates I-IV; Text-figures 1-5)

INTRODUCTION

THE freshwater or river dolphins of the family Platanistidae appear to be among the more primitive of living cetaceans. The family includes only four Recent species, which have typically relict distributions. The most aberrant of the existing species is the Ganges dolphin, *Platanista gangetica* (Lebeck), which inhabits parts of the Ganges, Indus and Bramaputra Rivers of India. A second species, the white-flag dolphin, *Lipotes vexillifer* Miller, occurs in Tung Ting Lake in central China and the adjacent parts of the Yangtze River some 600 miles above its mouth. Two species are Neotropical. The La Plata dolphin, *Pontoporia blainvillei* (Gervais), is found in the La Plata River and adjoining coastal waters between approximately 30 and 45 degrees South Latitude. It is the only platanistid that is not entirely restricted to fresh water. The Amazon dolphin, *Inia geoffrensis* (Blainville), ranges throughout much of the Amazon River system and also occurs in the Orinoco drainage. *Inia* appears to be most closely allied to *Lipotes*.

The Platanistidae first appear in the Miocene, and 12 genera are known from Miocene, Pliocene and Pleistocene marine deposits in North and South America and Europe. The fossil evidence suggests, therefore, that the platanistids were at one time a widespread and relatively successful marine group. An important factor contributing to their decline may have been competition with the more advanced delphinoid

odontocetes, which were well represented by late Miocene and Pliocene times. This apparent replacement of one adaptive level of organization by a more advanced type parallels in an interesting way the replacement of more primitive bony fishes by the teleosts in the Tertiary. A further similarity is the survival of the majority of the archaic bony fish remnants in fresh water habitats.

Although the living platanistids have been the subject of various taxonomic and anatomical studies, almost nothing is known of the details of their natural history. This paper presents observations on the habits and behavior of the Amazon dolphin in captivity. The study was carried out at Silver Springs, Florida, where two specimens captured in the upper Amazon in the vicinity of Leticia, Colombia, were kept alive for over a year. These individuals were the survivors of four specimens captured by an expedition sponsored by Florida's Silver Springs in February and March, 1956, and flown to Florida. Field studies made on *Inia* and the delphinoid *Sotalia* during this expedition have previously been published (Layne, 1958).

We made observations on the *Inia* at Silver Springs throughout the entire period of their captivity. The extreme clarity of the water in which they were kept and the manner in which they were maintained afforded ideal opportunities for observations. This was particularly true during the first two months following their capture, when they were kept under more natural conditions and isolated from the general public.

During their early captivity we observed the

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dolphins several times a week for periods ranging from one to five or six hours. Later we visited the dolphins at intervals of from one to several weeks. Usually, we watched the animals from the banks of the channel in which they were initially kept or from the roof of a "submarine" boat moored alongside the pen in the main spring to which they were later transferred. The roof of the boat was some 6 to 8 feet above the water and provided an excellent vantage point from which to observe the activities of the dolphins anywhere in the enclosure, either at or below the surface. The boat also had a deep well with portholes several feet below the water line through which we could make closer observations on the activities of dolphins while they were swimming under water.

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CAPTURE AND TRANSPORT OF SPECIMENS

Various means were employed by the Silver Springs party in an attempt to capture *Inia*. A net approximately 100 yards long, 10 feet deep and with 2-inch meshes, was used on several occasions in an effort to trap dolphins as they moved along the border of flooded jungles or pursued fish off points of land. The results were unsuccessful, as high waters made it difficult to confine the animals and individuals seemed to easily detect the presence of the net, possibly through echolocation, and avoided it without difficulty. One attempt was made to stun the animals by means of an underwater explosion in the hope that they could be more easily captured with the net or harpooned in a non-vital part of the body. The site selected for this attempt was at the entrance of a channel leading from the Amazon to some lakes about a mile north of the town of Leticia. This channel was regularly used by dolphins in moving back and forth between the lakes and the main river. The channel was blocked with the net at a point about 100 yards from its entrance to the river. As a dolphin approached the net on its way through the channel a single stick charge of dynamite was exploded underwater within a few feet of the animal. Although the *Inia* appeared to have been stunned by the blast, it escaped by swimming over the top of the net at a point between floats where the net sagged several feet below the surface.

It was the general opinion of the inhabitants of the region that capturing *Inia* alive would have been considerably easier during the dry season, when the animals could be trapped in shallow coves or narrow channels. They reported that *Inia* were not infrequently captured in fish traps during times of low waters.

Specimens were finally obtained by Indian fishermen who waited quietly concealed at the edge of the flooded jungles along watercourses frequented by the dolphins and harpooned animals that swam within range. On March 4, a fisherman harpooned a large male *Inia* about 7 feet in length and weighing approximately 300 pounds. The animal swam off and was later found about a mile away with the float and harpoon line entangled in some bushes along the edge of the flooded forest. It was hauled into a 16-foot boat and taken to the town, where it was placed in a large concrete fish pond. The following day a small female and male were secured near the spot where the first specimen was taken. All three animals were struck in the dorsal musculature at a point above and just behind the pelvis. The small male appeared to

have been more severely injured than the others, as he swam more slowly and laboriously when released in the pool.

The dolphins were loaded on board a plane on the morning of March 6, each receiving an injection of penicillin at the time. The two small individuals were placed in a small dugout canoe containing a few inches of water and covered with wet cloths. The large male was suspended from the roof of the cabin in a canvas sling and covered with a wet sleeping bag.

The attendants reported that all three animals struggled considerably en route to Florida. At one point in the flight, when the plane was at an altitude of 18,000 feet, the small male grew very weak, until finally no heartbeat could be detected. He was revived by artificial respiration and the administration of oxygen by means of an oxygen mask placed over the blowhole. The small female died during the flight. While dissecting this animal later, Dr. K. M. Backhouse found an abscess in the musculature of the neck, which might have been a secondary infection resulting from the harpoon wound and, together with exhaustion, a contributing factor in the death of the animal.

The plane bearing the dolphins arrived at the Ocala, Florida, airfield on the morning of March 7. The two surviving dolphins were transported by truck to Silver Springs and placed in a side channel off the main river. As the animals were being lowered into the water, the large male struggled free of his wrappings and swam off in a normal manner. The small male was noticeably weak and had to be supported in the water in order to breathe. He seemed to gain strength after being in the water a few minutes and began to swim weakly about without support, although he continually ran up into the shallows along the edge of the channel. Within an hour, he had weakened again and despite administration of oxygen through the blowhole and injections of antibiotics and B vitamins went into convulsions and died.

A fourth *Inia*, a small male, captured near Leticia in a manner similar to that of the others, was flown to Tarpon Zoo, Tarpon Springs, Florida, on March 11. He was held in a pool overnight at Tarpon Springs and transported to Silver Springs, a distance of about 100 miles, by car the following day. He appeared to be in good condition upon arrival and behaved normally when introduced into the channel with the larger male.

As is the general case with marine dolphins (Kritzler, 1952), none of the *Inia* offered any resistance to being handled when once out of

water. However, the large male struggled considerably when he was being captured for removal from the fish pond in Leticia. Several times a man attempting to hang onto the dolphin's tail stock was thrown completely clear of the water.

We have knowledge of a number of other *Inia* brought alive to this country subsequent to the four mentioned above. Nine of these specimens were received by the Tarpon Zoo. According to Trudi Jerkins, co-owner of that establishment, seven young and adult inias were successfully flown alive from Leticia to Tarpon Springs in 1956, a short time after the Silver Springs expedition had obtained theirs. These inias were also taken with harpoon and lived in captivity for varying periods of time, the maximum being about a year. The animals were kept in a fenced enclosure about 50 by 25 yards in a small pond. They were fed artificially but may have captured some natural food from time to time. The animals all died within a period of a few days. Death was suspected to have been caused by the accumulation of an organic insecticide in the pond as the result of aerial spraying of nearby citrus groves.

Another specimen obtained by the Tarpon Zoo was an old female captured at Leticia on March 18, 1959, and flown to Tarpon Springs a week later. Although the *Inia* appeared to be in relatively good condition on arrival, she died shortly afterwards from causes unknown. Starvation seemed to be ruled out as a possible factor in the death of this animal as it was reported to have fed well during the week it was held in a pond in Leticia. Tarpon Zoo also supplied a female *Inia* to the Fort Worth Zoological Park, Ft. Worth, Texas, in the spring of 1962. The Fort Worth Zoological Park also obtained a second female in July, 1962, from the Gulf Fish Hatchery, Inc., a Florida firm dealing in exotic fishes. This specimen was reported to have been taken by net in the upper Amazon.

In 1963, several additional live *Inia* were also brought from the upper Amazon for display at a tourist attraction at Homosassa Springs, Florida.

Upon their arrival at Silver Springs, the *Inia* were placed in a small side channel connected to the main spring and river. This area was well removed from human activity, thus the dolphins were relatively little disturbed during the early period of their captivity.

The section of the channel in which the dolphins were confined by means of blocking fences was about 300 yards long and varied from approximately 20 to 25 feet in width. The banks

were generally wooded and some portions of the channel were shaded during most of the day. The remains of an old foot bridge were located nearly midway between the two fences, and pools 4 or 5 feet in depth alternated with very shallow areas along the length of the stream. A prominent, shallow sand bar was situated a short distance below the bridge. Several weeks after the inias were placed in the channel, the bottom was dredged to provide a deeper passage between pools. The pools most utilized by the dolphins were located at the upstream fence, just above and below the bridge, and about 30 yards downstream from the bridge.

The bottom of the stream was sandy, although overlain with silt in most areas. The sides were generally more silty than the center. Beds of eel grass (*Vallisneria*) were frequent, and water-logged sticks, leaves and other debris were scattered about over the bottom. There was a moderate, steady current in the channel at all times, and water temperatures approximated 70 degrees F., with little seasonal variation. As in the main spring area and river, the water of the channel was exceptionally clear.

In June, 1956, the dolphins were moved from the channel to a large enclosure in the main spring area. This pen had dimensions of about 75 by 40 feet. Its depth ranged from about 5 feet near the bank to a maximum of approximately 10 feet in the deepest portion. The bottom was sandy and partially covered with large patches of eel grass. Shortly after the inias were introduced into the enclosure a mat of water hyacinths (*Eichornia*) was spread over about half of the surface to provide some shade for the animals. During the winter of 1956, the large male became increasingly aggressive toward the smaller individual and it became necessary to separate the animals in the enclosure by means of a fence. This arrangement was maintained until the death of the dolphins the following spring.

Conditions under which observations could be made were somewhat less satisfactory in the main spring than in the channel. There was a much greater disturbance level in the main spring. A bathing beach was situated adjacent to the pen, and numerous power boats passed within a few yards during the daylight hours.

HEALTH

The dolphins appeared to acclimate well to the conditions of captivity. The harpoon wounds healed without complications, and outwardly the animals remained in generally good health until just preceding their deaths the following year.

Shortly after they arrived the dolphins developed fuzzy yellowish patches, apparently a fungus growth, on the flukes, caudal peduncle and flippers. Smaller patches were also present on the snout of the small male and over one eye of the adult. The patches became less noticeable in about a week and soon disappeared entirely.

From time to time abrasions were noted on the snout and leading edges of the dorsal fin, flippers and flukes. These wounds were apparently caused by the dolphins rubbing against objects in the water, an activity in which they frequently engaged.

Both individuals also suffered from cracking of the skin, which was first observed on April 20. This condition was most severe on the dorsum between the blowhole and origin of the dorsal fin and appeared to be the result of sunburn, since the animals at this time were still being kept in the relatively shallow and extremely clear water of the channel and spent much of their time just beneath the surface. The back of the larger male was more severely affected than that of the smaller individual, whose skin was more heavily pigmented and thus probably better protected from the sun's rays. The area around the blowhole, which was well pigmented in both individuals, was not injured. It has been suggested (Layne, 1958) that the persistence of pigment around the blowhole, even in the fully grown, pale-colored adult *Inia*, may be an adaptation for preventing sunburn of that portion of the head regularly exposed above water in the course of breathing. In the natural habitat, the rest of the dolphin's body is probably protected from the sun by the general turbidity of the water. When the inias were transferred from the channel to the deeper water of the pen and a cover of water hyacinths was provided, the condition of the skin improved rapidly.

Both dolphins grew progressively darker during the period of their captivity. This increase in skin pigmentation was probably a response to the greater light intensity in the clear water in which the animals were kept. Similar environmentally-induced changes in coloration apparently also occur under natural conditions, as Jardine (1837) states that inias inhabiting rivers are paler than those in lakes. This trend is probably associated with the usually more turbid water conditions in rivers as compared to lakes.

The dolphins occasionally suffered from respiratory ailments. One such case occurred in the small male a few days after reaching Silver Springs. For a day or so he would give loud snorts when surfacing to breathe. Each snort would be accompanied by a discharge of glob-

ules of mucous-like material from the blowhole. The material, which would be expelled to distances of 5 or 6 feet, resembled the nasal discharge of humans suffering from a cold, being yellowish-white, highly viscous and possessing a faint odor. The captives also sometimes uttered similar snorts under circumstances which suggested that the sounds might have some communicatory function (see p. 102).

The small male died in March, 1957, after a year in captivity. On March 23 he appeared to be experiencing respiratory difficulty. The narial passages seemed to be clogged, although no discharge of material was noted at expiration. The dolphin also listed to one side when he came to the surface for air. He had eaten little or nothing for several days. The animal was captured with a net and given injections of penicillin and adrenalin intramuscularly. The following day the dolphin's condition had worsened. Although he seemed to have less difficulty in breathing than the day before, he swam sharply heeled over on the right side and was extremely bloated. As a result of the latter condition he had difficulty in submerging and remaining under water and would pop to the surface like a cork as soon as he ceased swimming movements. At this time he was removed to a stock watering tank where he could be more easily observed and cared for.

Despite administration of antibiotics and other treatment, the dolphin showed no improvement, and by the evening of March 28 there appeared to be no hope for recovery. The dolphin was transported by car to the J. Hillis Miller Health Center at the University of Florida where it was killed by over-anesthetization with ether.

An autopsy revealed several pieces of water-soaked wood in the stomach, congestion in the lungs, and an extensive hemorrhage in the brain, all of which might have contributed to the death of the animal. The hemorrhage in the brain involved virtually the entire right cerebral hemisphere and extended to the midbrain. Flukes, *Hunterotrema caballeroi*, were found in the air passages of the lungs, and later microscopic examination of sections revealed the presence of trematode eggs in the brain.

Additional records of endoparasites have been obtained from two other *Inia* that we have handled. Numerous round worms, *Anisakis insignis*, were present in the stomach of the young female that died enroute during the initial shipment of the dolphins to Florida. Specimens of the same species were also obtained from the stomach of the old female purchased from Tarpon Zoo in March, 1959.

The large male was found dead on the morn-

ing of May 10, 1957, after 15 months in captivity. Although he had ceased feeding for a short interval a week or so before, he had otherwise behaved in a normal manner until the time of his death. According to Dr. K. M. Backhouse, who later dissected this animal, death was apparently due to severe bronchial pneumonia involving both lungs.

MISCELLANEOUS PHYSIOLOGICAL DATA

A few physiological data were gathered incidental to other observations. Heart rate was measured on two occasions. An average of 60 beats per minute was recorded for the large male before he was removed from the plane after the trip from Leticia. The intervals between breaths during the period over which the heart rate was determined averaged 63 seconds, with extremes of 18 and 107 seconds. The heart rate of the small male shortly before death averaged 96 per minute, with extremes of 90 and 104. At the time of measurement the dolphin had been out of water for approximately two hours, although it had been covered most of the time with moist blankets. In view of the animal's weakened condition and other factors, it may be assumed that the heart rate recorded on this occasion is well above normal.

A rectal temperature of 97.4° F was obtained for the small male while he was being held in the stock watering tank for examination and treatment. The water temperature was 69° F. Another measurement was made when the animal arrived at Gainesville following a 40-mile trip from Silver Springs by automobile. The rectal temperature on this occasion was 96.9° F. The dolphin had been uncovered for several minutes before the temperature was taken and its skin was fairly dry. In both measurements the thermometer was inserted to a distance of only about 6 inches, thus the temperatures obtained may not have represented actual core values. They do, however, fall well within the range of cetacean temperatures cited by Kellogg (1928) and Wislocki (1933).

The small dolphin died much more rapidly under ether anesthesia than expected. As soon as the ether cone was placed over the blowhole, the animal clamped the lips of the blowhole tightly together and refused to take a breath for an abnormally long interval. The tempo of the dolphin's breathing became more rapid and regular after several breaths of ether and then it abruptly died. Lilly (1958) suggests that the breathing of cetaceans, as an adaptation to an aquatic habitus, is predominantly under voluntary control, which makes anesthesia difficult because the animal ceases to breathe as soon as

it loses consciousness. It is not certain that the rapid death of the *Inia* when given ether is explainable on this basis. The transition from irregular to rhythmic breathing observed might have indicated a shift from voluntary to involuntary regulation and death may actually have been due to the specific effect of ether.

Weights of certain organs of the small male, whose total length was 1,877 mm., were as follows: liver, 1,800 gms.; heart, 275 gms.; kidneys (both), 300 gms.; spleen, 23 gms.; lungs, 1,450 gms.; adrenals, 9 gms.; and thymus, 75 gms. The total length of the intestine (large and small together) was 105 feet. The brain weighed 525 gms., giving a brain weight/body length index of 88, a value markedly lower than those given for other cetaceans (Lilly, 1958; Kojima, 1951; Jansen 1952). A red blood cell count of 3,671,000 per mm³ was calculated by Elizabeth S. Wing from a sample obtained from the body cavity of the small male during the autopsy. Unfortunately, body weight was not recorded for this specimen.

GENERAL BEHAVIOR AND ACTIVITY

During the first week or so in captivity the dolphins confined their movements to the part of the stream above the large sand bar mentioned previously. Neither animal was observed to cross the bar and explore the section of the stream below until a channel was dredged through it. Thereafter, the dolphins occasionally ventured into the lower part of the stream, although they still spent most of their time in the section above the sand bar. When crossing the bar, they always remained in the deepest part of the channel.

The dolphins tended to restrict their activity to a certain part of the channel for a time and then shift to another. They would usually remain in a given pool for some time, swimming in slow irregular circles, often following the same path and rising to breathe in nearly the same spot each time, and then make a leisurely excursion up or downstream to another pool. Sometimes they remained in the second pool for an extended period, but more often returned in a short time to the original one to continue idly circling about. While swimming they would often probe the bottom with their long beak, and when in the pool next to the bridge they would frequently thrust the break into the crevices between the logs. The dolphins frequently settled on the bottom.

The animals were somewhat more active in the enclosure in the main spring area. They were observed resting on the bottom only once and showed a lesser tendency to confine their activity to a particular portion of the enclosure for

any length of time, although they would sometimes follow the same general path in swimming and surfacing for air for an interval of several minutes. The generally unoriented pattern of movements of the inias in the enclosure appears similar to that of a captive female bottlenosed dolphin studied by Schevill & Lawrence (1956).

Two observations were made that indicated a tendency of *Inia* to become habituated to a particular area. This was first demonstrated when the dolphins were moved from the channel to new quarters in the main spring enclosure. The upstream fence was removed with the intention of herding the animals up the channel to the new pen. However, it proved extremely difficult to drive them beyond the former limits of the fence. The second example of reticence to abandon familiar surroundings occurred when the fence that had been erected across the main spring enclosure to separate the two animals was lowered after the death of the small male. Although seen to explore the opening from time to time, the surviving animal did not venture into the other side for at least five days.

Wild *Inia* appear to exhibit positive rheotaxis (Layne, 1958), and the captives reacted similarly to even the relatively slight current in the channel. When the large male was first released into the channel he circled about nearby. When disturbed by a human swimmer he swam rapidly and unhesitatingly upstream until stopped by the fence. Since he had no knowledge of the stream at this time, his behavior seems to indicate a response to the current. Both inias showed a definite predilection for the upstream end of the channel, spending much of their time in the pool just below the fence. They would orient themselves into the current and maintain their position with slow strokes of the flukes. Whenever they rested on the bottom they invariably headed upstream. When alarmed anywhere in the channel, the dolphins would usually swim rapidly to the upstream fence. If frightened while swimming downstream they would often continue in the same direction with increased speed for a few feet but then nearly always turned and headed back upstream. If a human being in the water positioned himself between one of the dolphins and the upper fence the animal would become visibly agitated. It would finally rush past, swinging as far out to the side opposite the intruder as the width of the channel would permit, and take refuge in the upper end. Captive *Tursiops* and *Globicephala* exhibit a similar tendency to swim into a current and, at least in the case of the latter, may derive pleasure from the flow of the water over the

body (McBride & Kritzler, 1951; Kritzler, 1952).

One of the commonly observed activities of the dolphins was scratching or rubbing. Although they were seen to scratch or rub the body against the bottom or projecting objects as they swam about throughout the period of their confinement, they engaged in extensive periods of such activity for several weeks during the early period of captivity. The cause of the increased scratching during this interval may have been an irritation from what appeared to be a fungal growth on parts of the body, since a reduction in the frequency of scratching behavior coincided with the disappearance of the growth on the skin. On March 16 both animals were observed doing slow rolls while swimming slowly along and rubbing the dorsum and upper sides along the bottom. A week later they were found in the pool below the bridge, where they continually circled and scratched on a stick about a foot long that was sticking up out of the bottom. They would approach the stick swimming either on the back or upright and scrape the body with force sufficient to push the skin into prominent folds. Later they transferred their activity to the next pool downstream, where they spent approximately half an hour scraping their backs on the bottom. They would swim upside down for almost the entire interval between breaths and wriggle from side to side as they dragged their backs over the sand. The dolphins cleaned off a patch of sand about 15 feet in diameter by their actions. They next moved back to the original pool and continued scratching on the same stick as before.

The dolphins were again observed to be engaged in scratching and wallowing activity for long periods of time in the same pools on March 31. They also intentionally rubbed against projecting sticks in their sallies up and down the channel between the pools. A similar tendency to rub and scratch, even to the point of causing abrasions in some instances, has been reported for bottle-nosed dolphins and pilot whales in captivity (Townsend, 1914; Kritzler, 1949; McBride & Kritzler, 1951; Tavolga & Essapian, 1957).

The captive *Inia* exhibited no definite diel activity cycle. On the several occasions that they were observed at night, their general behavior and movements were no different from those seen during the daylight hours. They apparently slept for short intervals throughout the day. While in the channel, they would often settle to the bottom and lie motionless except for slight movements of the flukes. They invariably oriented with the head into the current and usually

selected a place where the current was strongest. It is possible that this behavior represented sleep, since the animals would sometimes rise slowly to the surface, breathe, then sink back to the bottom again. The trip to and from the surface was accomplished by little, if any, forward movement and was probably accomplished largely by altering the volume of air in the lungs through muscle contraction or relaxation, although flipper movement may also have contributed. Only on one occasion was an apparently sleeping individual observed in the enclosure in the main spring. In this instance, the large male was seen floating just off the bottom with his body forming an S-curve and only the tail in contact with the substrate. According to the observer, the dolphin remained in this position for some time. Both *Inia* occasionally yawned while swimming beneath the surface, and there seemed to be a general tendency for an increased frequency of yawning in the late afternoon. McBride & Kritzler (1951) noted similar behavior in a pregnant female *Tursiops* near parturition.

LOCOMOTION

As in the wild (Layne, 1958), the Amazon dolphins at Silver Springs normally swam at a very slow speed, averaging only between 1 and 2 m.p.h. The only times they moved with greater rapidity were when they were alarmed or feeding. On two occasions we were able to time individuals with a stopwatch over a measured course after they had been startled into swimming at what probably represented nearly maximum speed. The speeds attained in these instances were only 8 and 10 m.p.h. Wild *Inia* seen swimming under circumstances that suggested they were exerting themselves to their limits appeared to be traveling at about the same speed. A bottle-nose dolphin kept by Schevill & Lawrence (1953) in an enclosure with murky water usually swam at a speed of about 4.5 m.p.h. Free-swimming marine dolphins, however, often travel much faster, speeds ranging from about 12 to 34 m.p.h. having been reported (Petersen, 1925; Gray, 1936; Moore, 1953). On the basis of these data, the Amazon dolphin appears to be an exceptionally slow swimmer.

Jardine (1837) has also noted that *Inia* is neither as agile nor as powerful as marine dolphins and that *Platanista*, too, is generally slow and sluggish in its swimming habits, although it may move swiftly when pursuing fish. The apparently marked differences in swimming speeds between the platanistids and marine dolphins are correlated with the morphological features of the two groups. The long beak and well-developed, flexible neck of *Inia* and other

platanistids would appear to offer a severe impediment to rapid swimming because of the difficulty in preventing lateral displacements of the head as the animal moves swiftly through the water. The reduction of the rostrum together with the shortening and fusion of the cervical vertebrae in the advanced marine dolphins are probably among the important adaptive trends accompanying the development of fast swimming habits, an ability which may have contributed significantly to the eventual dominance of the delphinids over the platanistids in late Tertiary seas. The relatively large flukes and flippers of *Inia* also appear to be correlated with its slow swimming habits, since in a slow moving dolphin larger control surfaces are probably necessary to maintain maneuverability and stability. Howell (1930) has stated that the dorsal fin is less effective in maintaining equilibrium in cetaceans than in fishes, the flippers of the former probably being more important in this connection. Thus, the relatively poor development of the dorsal fin of *Inia* may be compensated for by the large size of the flippers (Pl. I, Fig. 1). Another distinctive feature perhaps associated with the mode of locomotion of *Inia* is the marked flexibility of the flippers as compared to those of fast-swimming marine dolphins in which they serve mainly as hydroplanes. On several occasions we observed the captive inias propelling themselves very slowly forward by means of a rowing-like action of the flippers, and an individual rising to blow with little forward momentum would aid its ascent with movements of the flippers.

When the captive *Inia* were swimming at the normally slow cruising rate, the flukes were moved through a vertical angle of approximately 20 degrees. Although the entire body pitched up and down with the strokes to some extent, the principal movement was confined to the tail stock and flukes. The point upon which the rear part of the body pivoted during swimming movements was in the approximate region of the pelvic girdle, as is characteristic of cetaceans in general (Slijper, 1961). The stroke rate of the flukes in slow swimming was about 1 every 2 seconds. On occasion, when the dolphins were swimming slowly, a distinct lateral component was added to the vertical motion of the tail stock and flukes, producing a somewhat oblique stroke. An apparently similar stroking action of the tail has been reported in other cetaceans (Beddard, 1900; Petersen, 1925; Kellogg, 1928).

Ordinarily the dolphins swam just below the surface, with the flippers held nearly horizontal and fairly close to the body. Slight adjustments in their position were made as the dolphins swam

along, but they were normally not moved extensively when an animal was proceeding on a direct course. When the dolphins swam near the bottom, the flippers were sometimes lowered and allowed to trail gently along the bottom. Turning was accomplished by throwing the body into a curve and through obvious employment of the flippers. Usually the inboard flipper was held more or less vertical while the outboard one was held more laterally and utilized in a rowing manner to help in the turn. The fish-tailing movements of the caudal peduncle seemed to be exaggerated when the animals were turning.

A particularly striking characteristic of the swimming of *Inia* is the pronounced mobility of the head. When the dolphins were progressing at the characteristically leisurely cruising pace, the head was in more or less constant motion in both horizontal and vertical planes. The head was generally swung from side to side through an angle of about 45 degrees, but was moved to a lesser extent in the vertical plane. Often the dolphins turned the head 90 degrees or more to the axis of the body in order to examine an object to the side or beneath them. On several occasions they were seen to reach back beneath themselves to pick up a fish or to prod an object on the bottom as they passed over it. At such times the skin on the throat was thrown into conspicuous folds. The flexibility of the head in an upward direction seemed to be more restricted than either laterally or ventrally.

The increased power for fast swimming appeared to come chiefly from a greater stroke rate and to a lesser extent from an actual increase in the amplitude of the individual strokes. The pitching movements of the body were more pronounced than in slow swimming, and the head was not moved so extensively. A dolphin swimming just slightly faster than the normal speed moved the flukes about 1 stroke per second; whereas at moderately fast, but not maximum, speeds the stroke rate was increased to approximately 2 per second. When braking after a spurt of speed, the dolphins arched the flukes and caudal peduncle strongly downward.

A frequent maneuver performed by the dolphins was the barrel-roll. This was usually done as they swam slowly along and without interruption of their progress. Occasionally one would perform this feat from a position of rest on the bottom, simply rising off the bottom with no preliminary forward movement, rolling, and then moving slowly ahead. Captive *Tursiops* also engage in this behavior (McBride, 1940).

The dolphins often swam upside down. They would remain in this position from 2 or 3 seconds to the entire interval between breaths and

often progressed more than 50 feet in this manner. When swimming upside down they seemed to perform the same movements as in normal swimming and to have about equal control over their speed and direction. In observing this behavior, however, we gained the impression that the use of the flippers was more exaggerated than in normal swimming. One individual was seen swimming on its back while carrying a stick in its mouth with its head bent at an angle of nearly 90 degrees. Another individual was observed to masturbate while in this position. Captive *Tursiops* also swim on their backs; Townsend (1914) believed that there was more lateral action of the tail in this position than in normal swimming. The latter may also have been true with *Inia*.

When swimming slowly, the dolphins would often probe the bottom or clumps of eel grass with the beak in a slow and deliberate manner. Ordinarily they kept to the deeper portion of the channel. Only once was one seen to move into shallow water. In this case, the small male, in apparent avoidance of the larger one, swam on its back into a bed of eel grass in water a foot or so deep, then rolled over, coming to rest on the bottom with the back out of water. It stayed in this position for a moment and then with powerful lunging strokes made its way back into deeper water. Sanderson (1956) states that *Inia* utilizes the flippers in making its way out of water across mud flats. The behavior just described is as close to that described by Sanderson as we have observed, and in this case the flippers did not seem to be employed to any great extent in moving out of the shallow water, although admittedly we were unable to observe the event in detail. The captive *Inia* we have observed out of water have been helpless and were apparently unable to move by the use of the flippers. Although the flippers may be of limited use in moving through shallow water, we are highly skeptical that they could function out of water in the manner described by Sanderson.

Only once during our observations of the dolphins did we see the flukes break the water during swimming. In this instance, both animals were observed to bring their backs high out of the water and give vigorous slaps with the flukes on the water surface. Our impression of this behavior at the time was that the action was purposefully performed, possibly as an act of communication or play. Dr. Kenneth Backhouse told us of observing the leader of a school of *Delphinus* leap into the air and slap the water with the flukes as the school passed a ship some 150 yards away. Captive *Tursiops* also indulge in this behavior (Townsend, 1914; Lawrence

& Schevill, 1954; McBride & Hebb, 1948; McBride & Kritzler, 1951), and it has been reported in wild *Tursiops gilli* and other delphinids by Norris & Prescott (1961).

Although wild *Inia* were occasionally seen to leap out of the water (Layne, 1958), this behavior was not observed in the captives, probably because of limitations of space or water depth. Marine dolphins jump frequently under natural conditions, and similar behavior has been reported in captivity (Townsend, 1914; Lawrence & Schevill, 1954). The frequency of spontaneous leaping in the wild and captivity, together with the prodigious feats of jumping performed by trained *Tursiops* and *Lagenorhynchus*, provide further indication of the greater speed, power and agility of the marine dolphins in comparison to the platanistids.

During the early period of captivity, the two dolphins frequently swam about in very close association. The young male was invariably the one to initiate this activity. He would swim up to the larger individual and position himself close beside it, with his head at about the level of the adult's flipper (Pl. I, Fig. 2). The sides of the bodies, flukes, or flippers were sometimes in actual contact as the pair swam about, often surfacing to breathe simultaneously. Although our notes are not specific on the point, we are under the impression that the smaller individual did not appear to be showing typical swimming movements at such times. Although there was some movement of the flukes, this may have been at least partly passive. This swimming behavior appears to resemble that type of assisted locomotion in cetaceans termed echelon-formation swimming by Kelly (1959) and which appears to be widespread among delphinids (Norris & Prescott, 1961). However, as we were not aware of this phenomenon while we were making our observations on *Inia* swimming together and our notes are not adequate to reconstruct the details of what occurred, the existence of echelon-formation swimming in *Inia*, though probable, cannot be considered as established.

BREATHING

Under natural conditions *Inia* have been observed to surface for breathing in three ways (Layne, 1958). When swimming at the normal, slow cruising speed, the dolphins rise to breathe with the body parallel to the surface. The top of the head generally breaks the surface first and then the upper edge of the back lifts into view. The entire performance is accomplished in a leisurely and deliberate manner. Under some circumstances the dolphins roll in order to breathe, in typical marine dolphin fashion.

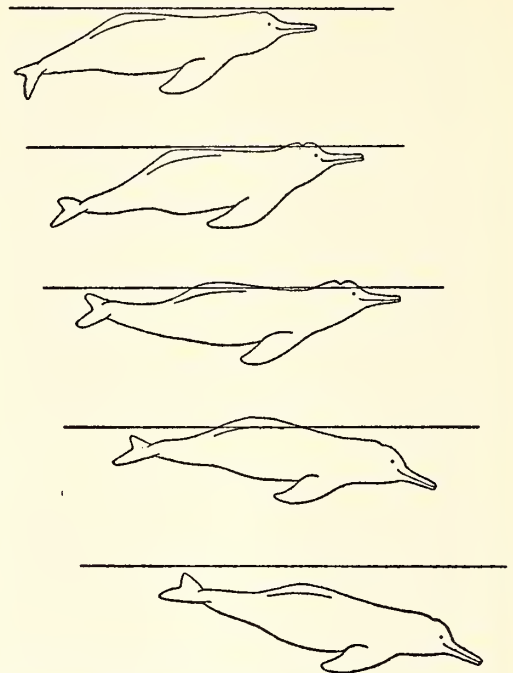
One type of roll, in which the animal arches high out of the water and re-enters almost vertically, appears to be associated with feeding activity, probably at some depth. The dolphins also roll to breathe when swimming rapidly. Under these conditions the body cleaves the surface in a low arc.

The captive *Inia* almost invariably utilized the horizontal method when surfacing to blow. Text-figure 1, drawn from a filmed surfacing sequence, illustrates this characteristic manner of respiration (Pl. II, Fig. 3). On several occasions when the dolphins had been alarmed and were swimming rapidly down the channel they performed somewhat abortive rolls, probably being prevented from executing the maneuver in the normal manner by the shallow depth of the water.

In typical surfacing, the head is brought out of the water only enough to expose the area about the blowhole; the beak does not ordinarily break the surface. The flexible neck permits the dolphin to lift the head to expose the blowhole when barely moving or even when motionless in the water. The closed blowhole is crescent-shaped, with the lateral points directed anteriorly. It has a more or less rectangular shape when fully opened. The opening of the blowhole appears to be brought about primarily by the forward movement and depression of the tissue mass associated with the anterior margin. In slow motion films of the action of the blowhole during the breathing cycle, we were unable to note the separate action of the plugs, vestibular sac and valve during the opening phase. When the blowhole was closing, however, the plugs, vestibular sac and valve could be seen operating in sequence. The size of the blowhole appeared to increase slightly, and the anterior margin to depress somewhat more, as inspiration progressed. Although our observations are not sufficiently detailed to permit critical comparisons, there appears to be no essential difference between the general functioning of the blowhole apparatus in *Inia* and that of *Tursiops* (Lawrence & Schevill, 1956).

The blowhole of *Inia* remains open approximately 2 seconds (1.2 to 2.2 seconds in 23 instances timed with a stopwatch during a normal breathing cycle). Wild inias appear to spend about the same amount of time at the surface (Layne, 1958). Expiration and inspiration are of about equal duration and are typically accompanied by a sighing or gasping sound. However, the normal sounds of the expiratory and inspiratory phases are distinctly different. Occasionally air is released with an explosive snort instead of the usual fainter sound.

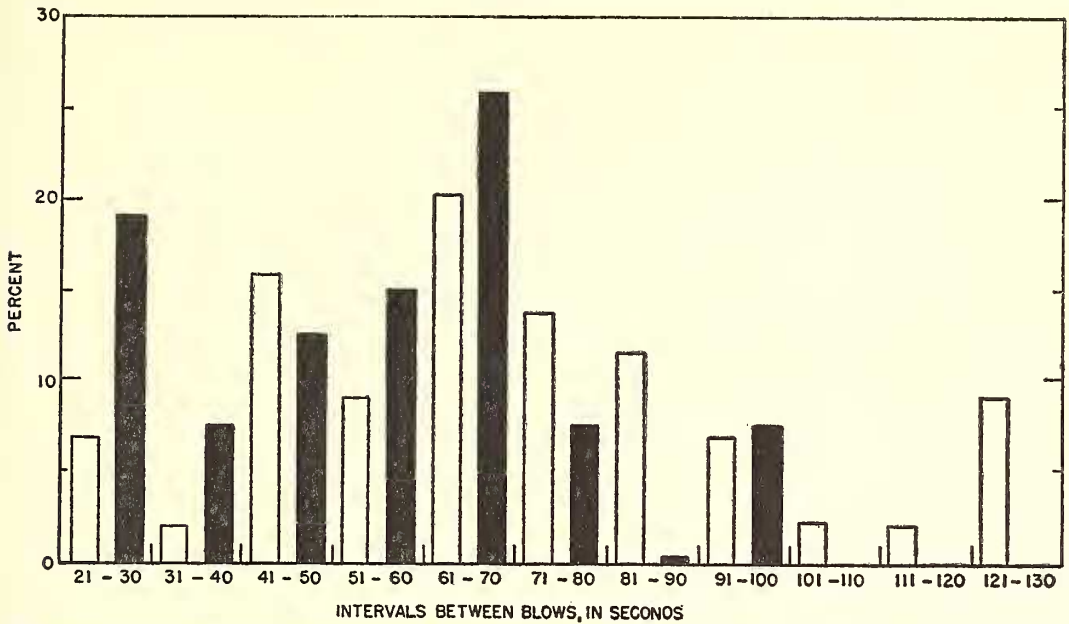
The duration of the normal blow of *Inia* is



TEXT-FIG. 1. Typical breathing pattern of *Inia*.

apparently much prolonged in comparison with marine dolphins. Lawrence & Schevill (1956) recorded the times of eight blows of a single *Tursiops* loafing at the surface and found that the duration of the blow under these conditions ranged from only .47 to .78 seconds. Presumably, an active swimming individual of this species would blow even more rapidly. The melon of *Inia* is particularly conspicuous and produces a marked bulge in front of the blowhole which appears to deflect water away from the open blowhole when the dolphin is swimming at the surface (Pl. II, Fig. 4). This seems to represent an adaptation associated with the typical horizontal method of surfacing and prolonged breathing interval.

Intervals between blows of Amazon dolphins recorded in the field ranged from 5 to 112 seconds and averaged 32 seconds (Layne, 1958). We also made a number of observations on the frequency of breathing of the captive *Inia* under various conditions of activity. All intervals were timed with a stopwatch. Twelve records for the large male, while it was still on board the plane following its arrival from South America, ranged from 18 to 105 seconds, with a mean of 60. Four records for this individual as it rested on the bottom and rose at intervals to breathe ranged from 18 to 94 seconds, with an average of 58. Forty-four records for the large male while it was swimming normally averaged 71



TEXT-FIG. 2. Frequency distribution of intervals between blows. Solid bars represent young male, open bars, the adult.

seconds (22-130) between blows. Twenty-six records for the small male under similar circumstances ranged from 22 to 98 seconds, with a mean of 54 seconds. The frequency distribution of the intervals between blows of the two captives during normal swimming activity is presented in Text-fig. 2. Although the data show no strong peaks at any particular frequencies, intervals between blows of greater than 80 seconds are relatively infrequent. These data also suggest that the small male had a higher breathing rate than the large one. Although approximately 32 percent of the intervals of the latter were over 80 seconds, only about 8 percent of those of the small dolphin exceeded this value. McBride & Kritzler (1951) note that infant *Tursiops* surface at nearly double the adult rate and attribute the difference to greater muscular exertion and heat loss in the young. A similar explanation may apply to the difference observed between the captive *Inia*.

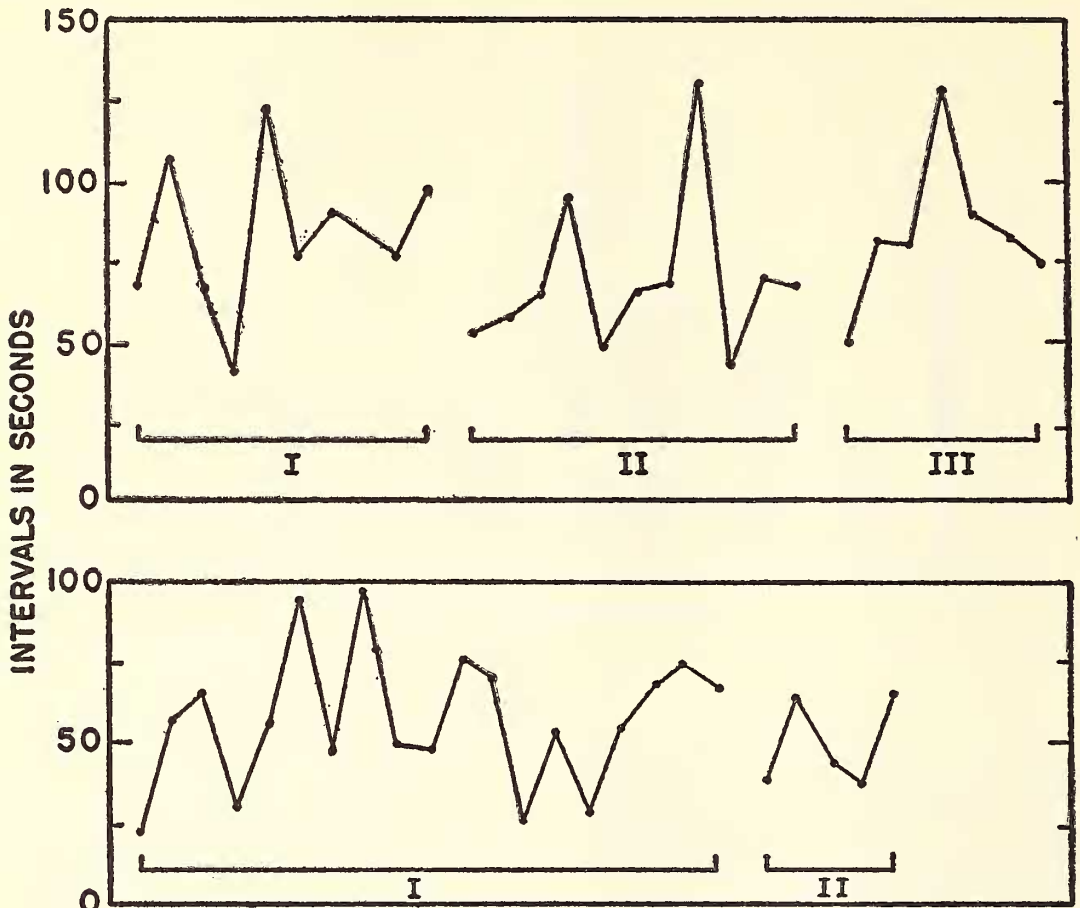
In a number of instances we recorded the lengths of intervals between a series of consecutive blows. Several of these series, obtained under normal swimming conditions, are presented in Text-fig. 3. Although there is no clear-cut pattern to the periodicity of blowing, there does appear to be at least a slight tendency toward a sequence of several shorter intervals alternating with ones of longer duration. A similar pattern of breathing was suggested by observations on wild *Inias* (Layne, 1958) and is clearly indicated

in data for some delphinids (Norris & Prescott, 1961).

On several occasions we saw the large male release air when he was still a foot or more beneath the surface when coming up to blow. The air appeared to be released instantaneously in one large bubble, and sometimes the dolphin gave a loud blow when his head broke the surface. Once after the animals had been placed in the main spring, we observed the lips of the blowhole of the small male relax and gape slightly as the animal approached the surface to breathe but was still several feet underwater. However, no air was seen to escape in this instance. When disturbed while breathing at the surface, the dolphins would instantly close the blowhole and submerge without completing the cycle.

Infrequently, as a dolphin came to the surface to blow, a spout of water or cloud of fine spray would accompany expiration. The former appeared to be the result of beginning expiration before the blowhole cleared the surface, while the appearance of spray seemed to be associated with a particularly vigorous exhalation. The latter phenomenon might represent cases in which water present in the vestibule was being blown out, as described for *Tursiops* by Lawrence & Schevill (1956).

Often during the early period of their captivity, the two dolphins surfaced to breathe in nearly perfect synchrony (Pl. III, Fig. 5). We



TEXT-FIG. 3. Intervals between blows in five breathing sequences.

also noted that when the animals were first placed in the enclosure in the main spring, they surfaced to breathe at the edge of the hyacinth mat or well out in open water. However, after a time they did not hesitate to push up through the mass of plants in order to expose the blowhole.

With the exception of Anderson's (1878) account for *Platanista*, details of the respiratory behavior of other platanistids are unknown. A captive *Platanista* observed by Anderson would rise slowly to the surface, exposing the blowhole and a portion of the back, blow and then slowly subside. Inspiration was so rapid that the blowhole seemed to close immediately after expiration. The entire breathing cycle took no more than a few seconds. A characteristic blowing sound, which is the basis of the various native names (e.g., sus, susu, sihoo, etc.) applied to this form, accompanied breathing. The intervals between breaths ranged from about 30 to 45 seconds. According to Anderson, wild *Platanista* surface to blow in the same manner but may

also plunge out of water upwards, forwards, and downwards, the snout being the first part of the body to appear. The usual surfacings are leisurely executed. On the basis of these observations, the mode of breathing of *Inia* and *Platanista* is apparently similar.

Hoy (1923) states that, according to the Chinese, *Lipotes* makes a "peculiar roaring sound," presumably when blowing, which is apparently of the same general nature as the sound produced by *Platanista* and *Inia*. This might indicate that *Lipotes* resembles *Platanista* and *Inia* in other aspects of breathing behavior as well.

Jardine (1837) states that *Inia* surfaces more frequently than marine dolphins, but does not give the evidence for this conclusion. McBride (1940) reports that *Tursiops* breathes about once every 30 seconds when sleeping and that the rate is slightly higher during normal activity. The mean values of respiratory intervals given for *Tursiops gilli* and *Orcinus orca* by Norris & Prescott (1961) do not differ greatly from those of *Inia*.

SENSORY CAPACITIES

Our information on sensory capacities is based upon observations of the behavior of the dolphins in various situations in which a particular type of stimulus seemed to be predominant. If the animal altered its behavior in a manner that seemed appropriate at the time the stimulus occurred, it was generally considered to be responding to the stimulus in question. For example, if a pebble was thrown into the water behind a cruising dolphin and the animal then suddenly speeded up its swimming, it was assumed that hearing and not vision was the sensory pathway involved. In actuality, many observations could not be given so obvious an interpretation. The increasing evidence of truly remarkable sensory phenomena in diverse kinds of animals, of which echolocation in marine odontocetes is an example, clearly illustrates the necessity of exercising great caution in drawing conclusions about the kinds, efficiency, and relative importance of the sensory modalities of an animal on the basis of general observations alone.

The principal sensory pathways utilized by the Amazon dolphin to obtain information about its environment appear to be vision, hearing and touch.

Vision.—A trend toward the reduction of the eyes, presumably correlated with life in turbid waters, is evidenced by the living representatives of the Platanistidae. This trend reaches its extreme development in *Platanista*, which is believed to be totally blind. A captive observed by Anderson (1878) would bump into the sides of its container when swimming about and showed no response when objects were passed rapidly before its eyes. Morphological evidence for absence of sight in this form is the lack of a crystalline lens and a rudimentary optic nerve. Numerous glands and structures resembling touch receptors of the skin occur in the conjunctiva, suggesting that the eye has become secondarily adapted to a tactile function (Anderson, 1878). Other than that it has small eyes (Burmeister, 1864-69), nothing is apparently known of the status of vision in *Pontoporia*. Allen (1938) states that the eye of *Lipotes* is very small and degenerate and that the dolphin is blind or nearly so. The latter conclusion appears to be based on the general appearance of the eye rather than upon actual observations of living individuals, although Hoy's (1923) brief account of the feeding habits of the white-flag dolphin suggests that sight may be of little importance.

Although the eyes of *Inia* are reduced as in other platanistids, they nevertheless appear to be completely functional. Gross reactions to light

were noted on two occasions. When the large male was being photographed in the dimly-lighted interior of the plane after its arrival at Ocala, it jerked convulsively each time a flash-bulb was discharged. After the dolphins had been in captivity two days, we visited them at night. Approaching the channel quietly in the dark, we waited until the dolphins came close then turned on our flashlights. As soon as the lights shone on them the animals panicked and swam rapidly away. Within a few minutes, however, they became accustomed to the lights and behaved in normal fashion.

Although the extent to which underwater vision serves *Inia* in the generally murky waters of its natural habitat is uncertain, the captive dolphins appeared to employ their eyes underwater to a considerable extent. When they were cruising about in the channel or pen in the main spring, they often seemed to be engaged in carefully scanning the bottom as they passed over it. Frequently they would reach down almost perpendicular to the body axis, or actually back under the body, to seize a dead fish, stick, old paper cup, or other object lying on the bottom. The dolphins appeared to sight such objects, which were often partially buried or nearly hidden by vegetation, from a distance of at least 2 feet. On one occasion an *Inia* was seen to swim up to investigate a small leaf, not more than an inch in length, that was floating on the surface. Many of the activities involved in play appeared to be mediated by vision, and the animals seemed to watch the observer when being fed from the hand. While in the enclosure in the main spring, the small male was often attracted by persons swimming outside the fence, usually at least 50 feet away, and would swim to the fence as if to watch them. Reed Parham, a Silver Springs employee, told us that on one occasion he quietly swam underwater to the dolphin pen at a point along the fence where he was hidden from the animals inside by a thick screen of eelgrass. He then carefully thrust his hand through the vegetation and moved his fingers. At once the small dolphin began to swim directly toward him. When a few feet away, the animal appeared to close its eyes but continued to approach slowly, performing the characteristic head swinging movements. The interpretation of this observation is not clear. The general behavior of the dolphin suggested that he had seen the hand when it appeared. However, the fact that the animal appeared to close its eyes when coming close yet continued on a direct course offers the possibility that echolocation might also have been involved.

Although wild inias sometimes bring their

heads far enough out of water during surfacing to expose the eyes and appear to examine their surroundings (Layne, 1958), such behavior was not observed in the captives. Nor did we find during the course of our study that the dolphins responded visually to objects above water when their eyes were submerged. One way in which this was tested was to wave a white handkerchief tied to the end of a stick a few inches above the water when a dolphin was approaching. In no case did either animal show any indication of being aware of the fluttering cloth just above its head, even as it passed beneath it. If the handkerchief was slowly and gently lowered into the water next to the bank while the dolphins were at the far end of the channel and held motionless except for movements caused by the current, the animals would seem to become aware of its presence from some distance away as they swam back down the channel. They would turn their heads in the direction of the handkerchief as they passed by at a distance of 5 or 6 feet. Townsend (1914) likewise found no evidence that *Tursiops* responded visually to objects above the surface when its eyes were under water, the dolphins he observed paying no attention to a fish suspended 2 inches above the surface.

The dolphins sometimes appeared to swim with the eyes closed during the day, although because of the small size of the eyes and their greyish coloration under water, it was difficult to be certain of this point. However, when the small male was being kept in the small tank before his death he sometimes surfaced to breathe with the eyes closed. This individual gave no response to a touch on the skin around the eyes nor on the eye itself. In contrast, Kritzler (1952) found that stranded pilot whales, *Globicephala*, were very sensitive to a touch on the skin around the eye and would immediately close the eye when thus stimulated.

In comparison with such marine dolphins as *Tursiops* and *Globicephala*, *Inia* does not appear to be a less visual animal to any significant degree. McBride & Hebb (1948) state that *Tursiops* uses its eyes both in and out of water, although it is not always easy to determine whether vision or audition is being utilized under water. Schevill & Lawrence (1956) noted that a captive individual studied by them used vision to locate fish at close range but apparently had difficulty in discrimination. Both *Tursiops* and *Globicephala* appear to have relatively keen vision above water and may employ the eyes in this way to a greater extent than *Inia*. This certainly appears to be true in the case of captives. Captive bottle-nose dolphins frequently thrust the head out of water or

"pitch-pole" out in order to examine their surroundings, and the remarkable ability of trained individuals to catch and throw objects with great accuracy further attests to the acuity of above water vision. McBride (1940) credits individuals with apparently being able to see moving objects at a distance of 50 feet. Schevill & Lawrence (1956) noted that a captive *Tursiops* looked above water to inspect its surroundings with greater frequency during the early period of confinement than later, and according to Kritzler (1952) a captive pilot whale was also apparently able to associate what it saw above water with discrete situations. Observations of wild *Tursiops* herding mullet toward steep banks in an endeavor to trap them (Kritzler, 1952) and killer whales scrutinizing ice floes for seals (Norman & Fraser, 1949) indicate that marine cetaceans may use their eyes above water under natural conditions.

Hearing.—The impression gained from our experiences with the captive inias is that, as in the case of marine cetaceans, hearing is probably the most important sensory faculty possessed by these animals. Several observations suggested that the dolphins could hear above-water sounds, but were less sensitive, or acclimated more readily, to these than to sounds made in the water. The large male was seen to flinch violently at any loud sound when he was out of water and being transferred from the plane to the springs following his arrival from South America. Also, on the second day in captivity this individual reacted in a similar manner when a person standing on the bank some 15 feet away closed a camera case with a loud click. The dolphin was swimming below the surface at the time. On later occasions, however, neither dolphin exhibited any response when under water or at the surface for air to such sounds as the rapping of sticks together, clapping or the blowing of a small horn, although the same sounds if made under water would inevitably send the animals off to another part of the channel in panic.

The dolphins were extremely sensitive to under-water sounds; they invariably reacted to such sounds with a startle or flight response—the animal giving a convulsive twitch and immediately accelerating its swimming. A similar response to underwater sounds has been described for *Tursiops* and *Stenella* by Kellogg & Kohler (1952) and Kellogg (1953). The dolphin would always continue on the same course, at least initially, even though the sound came from in front. The dolphins reacted in this way to even the slightest disturbance in the water. A cigarette, a match stick, or small piece of paper falling on the water within 10 feet of an animal,

slight movements of a small hollow pipe stuck into the bottom at the edge of the channel, and insects touching the surface of the water a few feet away were among the stimuli eliciting the startle response.

The inias were remarkably good at localizing the source of a sound. After a short time in captivity, they became conditioned to the splash of a fish being thrown into the water at feeding and would immediately swim rapidly to the source of the sound from any place in the channel. If at such times when the animals were excited and responsive, a stone was tossed into the water or the surface slapped with the hand or a stick, the dolphins would swim unerringly to the precise point from which the sound emanated, even though there were no ripples or other sign to mark the spot by the time they arrived in the vicinity. Natives in the Amazon region report that *Inia* can often be lured close to a boat by slapping the water with a paddle. Captive bottle-nose dolphins also respond readily to a slap on the water and localize the sound with great precision (McBride, 1940; Lawrence & Schevill, 1954; Schevill & Lawrence, 1956). Wild *Tursiops* may also locate prey in this way as well.

Field data and the observations made on the captives leave no doubt as to the extremely good auditory acuity of the Amazon dolphin and its refined ability to accomplish passive localization of a sound source. Although our evidence is admittedly circumstantial, we strongly suspect that *Inia* also possesses the ability to utilize active echolocation as one of its auditory orientation mechanisms. Several times during attempts to capture wild inias with a large net in a turbid channel or lakes near the Amazon, individuals seemed to perceive and avoid the net under conditions that seemed conclusively to rule out the possibility that vision was involved (Layne, 1958). The nature of the head movements often made by the captive dolphins when swimming about is also suggestive of the use of echolocation. When the dolphins were idling along the head was usually in motion. Movements in a horizontal plane predominated, the head being swung from side to side through a fairly broad arc, although it was also moved up and down to some extent. If the animal swam on its side, the nodding component of the head increased. The extent of head oscillations was keyed to the activity of the dolphins. When the animals were in an excited state, as during feeding or when disturbed, the head movements became more pronounced and rapid. An increase in the frequency of head-fanning was also observed as a dolphin approached a fish or other object that had been thrown into the water. In such instances

the dolphins would often reduce their speed during the last few feet of their approach and move forward slowly while sweeping the head vigorously from side to side. If the target object was settling rapidly, the general direction of the head oscillations would sometimes seem to lag somewhat behind the object. An observation that may indicate similar behavior in wild *Inia* has previously been described by Layne (1958). In this case an *Inia* was seen to submerge, and a short time later a small fish jumped from the vicinity in which the dolphin had been. An instant later the open jaws of the *Inia* appeared, wavered back and forth a few times, then disappeared again. The general impression gained from these events was that the dolphin had been approaching the fish very slowly and engaging in the same head-wagging behavior as observed in the captives.

Head movements apparently similar to those described for *Inia* are associated with echoranging by the bottle-nose dolphin (Schevill & Lawrence, 1956; Kellogg, 1958, 1959). Kellogg (1960, 1961) has termed this behavior "auditory scanning" and states that it occurs only while a porpoise is emitting trains of sound pulses. The significance of this behavior apparently lies in the increased precision of binaural localization in determining the direction from which echoes are coming. The seemingly close similarity of both the head movements of *Inia* and the conditions under which they are exhibited to those of echoranging *Tursiops* provides perhaps the most convincing evidence for the use of echolocation by the former. The recordings made of *Inia* vocalizations possessed a great deal of background noise and were difficult to interpret. In our study of these recordings we were unable to identify sounds of the type associated with echolocation in *Tursiops*.

Touch.—Tactile sensations are evidently important to cetaceans. Captive specimens of *Tursiops* and *Globicephala* frequently engage in rubbing their bodies against other animals or on inanimate objects. In some cases this behavior may be the result of irritations of the skin, but in others the animals appear to derive sensual pleasure from the activity (Kritzler, 1952; Lilly, 1961.) As noted previously, *Inia* exhibits similar tendencies.

Reference has been made earlier to the manner in which the dolphins would often probe and stir the bottom with the beak as they swam along or use it to explore the crevices of the old bridge in the channel. This use of the beak suggests that it may have an important function as a tactile organ. This supposition is further

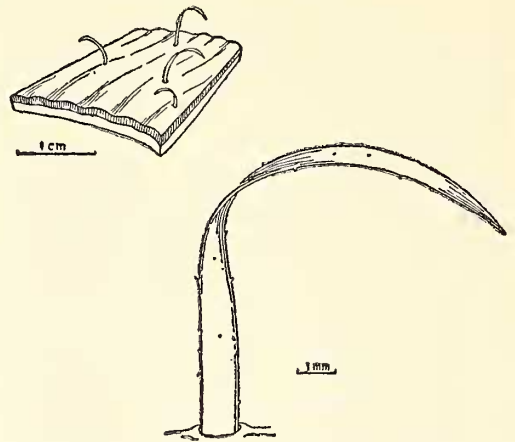
strengthened by the presence of numerous stout hairs on the beak, a characteristic in which *Inia* differs from all other cetaceans. These hairs are flattened, relatively non-tapering, and possess a slightly spinulose surface (Text-fig. 4). They are usually erect at the base but may be bent over at the tip. The tip is sometimes uneven, as if from wear. Each hair is set in a small pit and appears to be rather freely movable. The morphological nature of these hairs strongly suggests that they are specialized for a tactile function and may thus increase the over-all efficiency of the beak for this purpose. Among the other genera of platanistids, both *Platanista* and *Lipotes* also utilize the beak for probing and stirring around in the mud. Of interest in this connection is the fact that the trigeminal nerve was well developed in zeuglodonts and some squalodonts and was probably associated with a good sense of touch in the muzzle area (Kellogg, 1928). As the squalodonts may be close to the ancestral stock of the Platanistidae, the presumably highly developed tactile sensitivity of the beak in the freshwater dolphins might be regarded as a primitive as well as an adaptively significant feature.

TAMENESS AND LEARNING ABILITY

During the early period of captivity, the dolphins would not allow any one in the water to approach them closely. They would become visibly agitated when the observer was still 50 or 60 feet away, and their minimum flight distance was approximately 10 feet. Moreover, they ordinarily swam off in alarm before the observer, even though moving slowly and cautiously, could get that close. When forced to swim past a person in the water, the dolphins would keep as far away as possible and roll onto the side and with the back directed toward the human. The two individuals often stayed close together at such times.

By the end of three months in captivity, the dolphins had grown quite tame. Both individuals would readily swim up to a person in the water at feeding time. The small male would take fish from the hand without hesitation. The larger, however, was less bold and would accept a fish only if the feeder released it and allowed it to float a few inches from the hand. The larger male also avoided being touched, while the small one permitted himself to be patted and stroked. He would also allow a human to climb upon his back and would follow a person around the pen at feeding time. On one occasion, he attempted to initiate play with an observer in the water with him.

The dolphins were quick to note the presence



TEXT-FIG. 4. General and detailed views of bristles on the snout of *Inia*.

of new inanimate objects in their environment or changes in the relations of those already present. Their first reaction to a strange object was often one of fear and avoidance, and they frequently seemed to regard such an object with suspicion for some time after its appearance. Often when alarmed the pair would "close ranks" and remain together until the disturbance was removed or they became acclimated to it. McBride & Hebb (1948) have described similar behavior in *Tursiops* and point out that the degree to which such visually aroused fears are exhibited and their persistence show a relationship to phylogenetic development. The reaction of *Inia* to strange objects may not, however, be as pronounced as that of the bottle-nose dolphin.

One instance of a fear response to another animal was observed while the dolphins were in the channel. It was noted one day that the animals had begun to avoid the vicinity of the old bridge. Even when hungry, they were reluctant about coming to this area for food, and after seizing a fish would promptly swim to another part of the channel to eat it. A few days later a 4-foot alligator (*Alligator mississippiensis*) was discovered living in a hole beneath the bridge. The dolphins continued to avoid the area for some time after the reptile had been captured and removed. The behavior of the captives in this situation suggests the possibility that caimans may be one of the natural predators of *Inia*. McBride & Hebb (1948) describe behavior of *Tursiops* in the presence of tiger sharks (*Galeocerdo cuvieri*) that also suggests response to a natural enemy.

The *Inia* were initially induced to feed by throwing fish into the water near them. Within a few days they learned to associate a splash with

feeding and would come from distant parts of the channel in response to a slap on the water with a hand or stick. The speed with which the animals learned to associate this sound signal with feeding cannot entirely be attributed to rapid learning ability, as they probably possess an innate tendency to utilize splashes in localizing prey. No effort was made to give the animals more complex training.

When in the enclosure in the main spring, the dolphins exhibited considerable curiosity about the activities of swimmers nearby. The young male was particularly inquisitive and would often swim along the fence trying to keep as close as possible to a swimmer on the outside. Wild *Inia* also appear to be inquisitive and may closely approach boats and appear to look above water to examine the occupants (Layne, 1958). However, if persecuted they may become shy and alert to signs of danger. Lamb (1954) observed the rapid disappearance of a school from around a boat when a rifle was brought on deck. Lamb also gives another account of the way in which wild *Inia* may associate themselves with human activities. In this case, a dolphin would appear on the fishing ground of a native fisherman, presumably in response to the rapping of a paddle on the side of the canoe and a peculiar whistling call. The animal would then accompany the boat, holding a station 50 to 100 feet away on the deep water side and apparently scaring fish back into shallow water or in some instances actually onto the beach. Alpers (1961) summarizes information on marine delphinids giving assistance to humans engaged in fishing or whaling activities.

Data on several species of smaller marine odontocetes indicate that, although species differences do exist, these animals are in general easily tamed and learn rapidly (Brown & Norris, 1956; Brown, 1960; Hediger, 1952; Kritzler, 1952; Lawrence & Schevill, 1954; McBride, 1940; McBride & Hebb, 1948; McBride & Kritzler, 1951). There is, however, little information available on the actual time taken for wild-caught individuals of these species to become tame and to learn particular tasks, although Brown (1960), Kritzler (1952), McBride & Kritzler (1951), and Lawrence & Schevill (1954) give some data on these aspects for *Tursiops* and *Globicephala*. On the basis of the present observations, *Inia* does not appear to differ in any significant degree from the marine forms in the rapidity and extent to which it becomes tame nor in the general development of its learning ability, at least with respect to such simple things as taking food from the hand and responding to a sound as a signal for feeding. Although no effort was made to give the Amazon

dolphins the more complex type of training that some of the marine odontocetes receive in the various oceanariums in this country, we believe that *Inia* would show comparable learning capacities in those tasks that did not depend upon speed and agility, in which respects it is much inferior to forms like *Tursiops*.

FEEDING BEHAVIOR

Although the Amazon dolphin has been considered to be entirely piscivorous (Jardine, 1837; Kellogg, 1940), there are few data on its food habits in the wild. The stomach of a specimen from the Rio Guapore in Brazil examined by Natterer contained the remains of fish (Pelzeln, 1883), and *Inia* have been observed in apparent pursuit of fish (Layne, 1958). Additional information on foods was provided by the stomach contents of the small female that died en route to Florida from Colombia. This animal was captured on March 5, held overnight in a small fish pond, and loaded on the plane for transport to the United States the following day. Since there was no evidence that she had fed while in the pool, the stomach contents were presumed to represent feeding prior to capture.

The stomach of this specimen contained about 1½ quarts of fish remains. The bodies of several of the fish were nearly intact, though badly crushed, whereas the rest were fragmentary. The fish were judged to have ranged in size from about 4 to 8 inches and were either all of the same species or of closely similar types. Several of the more complete specimens were tentatively identified as being probably of the genus *Myleus*, one of the serrasalmine characins closely related to the piranhas. In addition to the fish remains, the stomach contained some insect fragments, chiefly beetle elytra and wings, a large seed, and a small amount of vegetation. The latter consisted of rather compact balls of what appeared to be the linear leaves of an aquatic plant. The insect and plant material comprised only a very small amount of the material in the stomach and in all probability resulted from accidental ingestion.

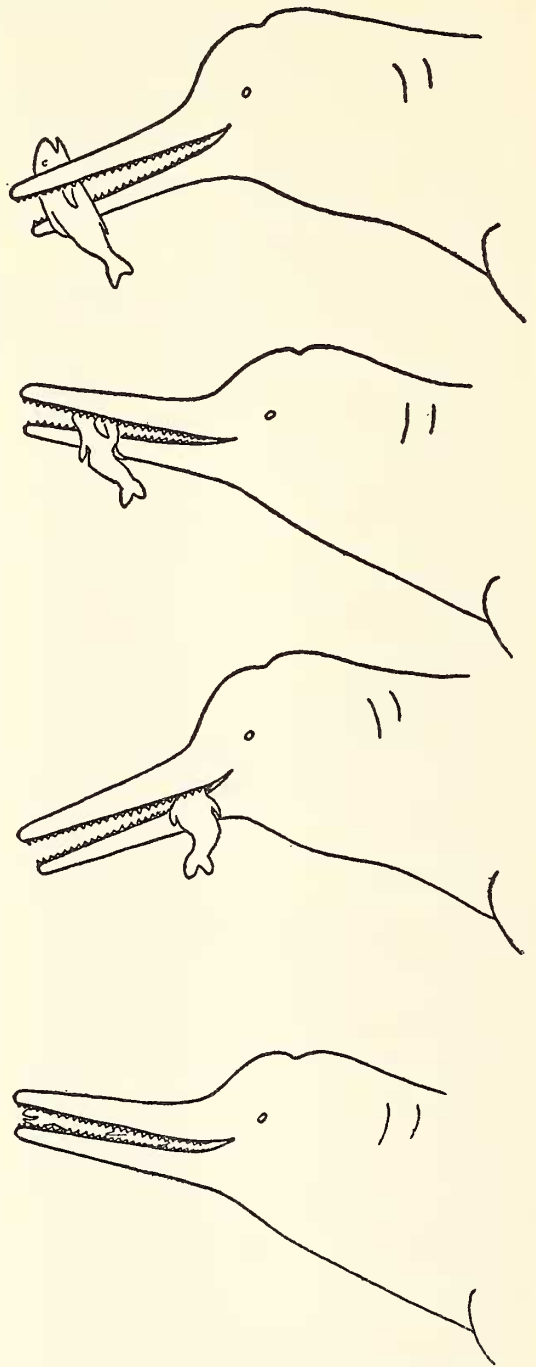
The captive *Inia* were initially fed on live minnows and sunfishes about 5 or 6 inches in length. The fish were thrown into the water near the dolphins with enough force to stun them and thus make them easy prey for the cetaceans. The large male fed on fish offered in this way the day following his arrival at Silver Springs. By the next day he had learned to associate the smack of the fish on the water with feeding and would come readily from some distance away upon hearing the sound. Although he would respond to the splash from a distance of 25 feet,

he did not appear actually to detect the fish until within 6 to 10 feet. If a fish recovered and swam off before the dolphin arrived, he would often circle the area in search of it.

As soon as the dolphins were feeding well on small fishes, their diet was changed to dead blue runners (*Carangidae*) and mullet (*Mugil*) which were obtained fresh daily from a local market. Together, the dolphins consumed between 20 and 35 pounds of fish daily. At first they were fed at frequent intervals throughout the day, but later their feeding schedule was reduced to a single feeding a day. When on a multiple feeding schedule, the dolphins usually showed greatest interest in food at the first feeding in the morning, but they would continue to accept food during the remainder of the day. The pair would usually consume about 5 pounds of fish at a feeding. When hungry, the dolphins were extremely responsive to a splash made when a fish was thrown into the water and would swim rapidly to the spot from any part of the channel. Sometimes they would become quite excited during the feeding period and would blow more frequently and hurriedly than normally. They often seized the fish at the surface before it began to sink or as it floated toward the bottom. They would also regularly pick up fish from the bottom, sometimes only to play with them but at other times to consume them. In many instances the fish had laid on the bottom for some time and had become nearly covered with silt.

The dolphins showed a preference for fish under a foot in length. The manner in which a fish was consumed was quite characteristic (Text-fig. 5). Almost invariably the dolphins would seize their prey with the tip of the forceps-like jaws (Pl. III, Fig. 6). The fish was then allowed to slip to the rear of the jaws where it was moved from side to side and vigorously chewed (Pl. III, Fig. 7). It was then manipulated into a longitudinal position in the jaws and swallowed headforemost. Occasionally, a dolphin would make a sharp turn to aid in swinging the fish into the proper position for swallowing. Immediately after swallowing a fish, the dolphins would often make short, quick nodding movements with the head. The captives always swallowed their food underwater, although wild *Inia* have been observed apparently consuming their prey at the surface (Jardine, 1837; Layne, 1958).

When swimming rapidly, the dolphins would occasionally seize a fish at the rear of the jaws rather than the tip. Sometimes an individual would carry a fish in the jaws for a minute or two, even surfacing to blow, before swallowing it. While carrying a fish in this manner, the dolphins would frequently toss it about in the



TEXT-FIG. 5. Sequence showing typical method of grasping, chewing, and swallowing a fish utilized by *Inia*.

jaws and occasionally even release it and allow it to drift some distance away before retrieving it with a slow, deliberate movement. When passing the fish to the rear of the jaws for masti-

cation the dolphins often allowed it to drift passively back into position rather than manipulating it with the jaws. The rather careless manner in which dead fish were usually handled by the captives after the initial bite suggests that perhaps in natural feeding *Inia* ordinarily cripples or kills its victim with the first bite so that there is little danger of it escaping while being maneuvered into position for crushing and swallowing.

While they were in the channel, the *Inia* always swallowed the fish entire after thoroughly chewing it. After they had been transferred to the pen, however, they showed a tendency to break up the fish into several pieces before swallowing. Sometimes the head was discarded.

We observed only one instance of natural feeding. This occurred while we were watching the large male with flashlights on the third night after he had been put into the channel. The animal broke the surface several times and once swam rapidly up to the bank as if in pursuit of something. A short time later it was seen carrying a fish about a foot in length. The fish appeared to be either a gar (*Lepisosteus*) or pickerel (*Esox*). The dolphin swam from below the bridge to the upper end of the channel with the fish held crosswise in its jaws but when it came back down the channel past the point from which we were watching the fish was gone. We could not determine whether the dolphin had dropped or swallowed it. A few minutes later the dolphin caught a gar about a foot long. The manner of capture was clearly observed. The fish was suspended motionless in the water when the dolphin approached. The latter did not increase its speed or show any other indication of being aware of the fish's presence until nearly abreast of it and about 2 feet away. It then swung its beak around in a deliberate motion and neatly seized the fish with the anterior part of the jaws about 2 inches back from the tip. The fish made no effort to escape until actually gripped in the dolphin's jaws. The *Inia* held the gar crosswise in the mouth and proceeded to shake it vigorously. It then released the fish which, although badly crippled, swam feebly away. A short time later the *Inia* captured another gar of about the same size as the previous one, possibly the same individual. Again the dolphin seized the fish with the front of the jaws and shook it terrier fashion. This time, however, it passed the fish to the rear of the jaws, chewed it vigorously, flipped it lengthwise in the mouth, and swallowed it headfirst.

Although no further instances of natural feeding were observed, an *Inia* would occasionally be seen to "track" a small fish swimming across

its path but without making any effort to capture it. From time to time dead fish, including sunfish (Centrarchidae), eel (*Anguilla*), catfish (Ictaluridae), and gar and water snakes (*Natrix*) were found in the dolphins' pen in the main spring. The animals had presumably been killed by the *Inia*, but there was no sign that the dolphins had made any effort to consume them.

Almost nothing is known of the feeding behavior of *Inia* under natural conditions. Field observations have indicated that the dolphins may forage either at some depth or near the surface and that the prey may be caught either by direct chase or slow stalking (Layne, 1958). The type of fishes found in the stomach of the small female also supports the contention that the dolphins may feed in the pelagic zone. The captives showed no hesitation in taking dead fish at the surface or while floating toward the bottom, and the observed captures of live fish occurred at intermediate depths.

As noted above, however, the captives frequently swam along near the bottom and would probe and dig in it with the beak. They would frequently pick up an object and toy with it and often ate dead fish off the bottom. It is possible that *Inia* forages in a similar manner in its natural environment. In fact, its small eyes and the generally turbid conditions of the waters it inhabits suggest that it may feed extensively in this manner, using the long beak to locate and dislodge bottom-dwelling fishes. The flexibility of the neck probably permits the beak to be used more effectively, and its vestiture of hairs probably increases its tactile sensitivity.

Wild *Inia* apparently capture and manipulate their prey in the same way as do captives. Circumstantial evidence for this was provided by the old female obtained from Tarpon Zoo. In this specimen, the teeth in the part of the jaws usually employed by the captives in seizing their prey were broken and worn, in distinct contrast to those in the remainder of the tooth rows (Plate IV, Fig. 8).

The nature of the dentition of *Inia* is clearly correlated with its mode of feeding. The anterior teeth are simple, conical structures; whereas the posterior series in each jaw are broad and heavy and have a rugose surface and a prominent internal projection. The form of the posterior teeth of *Inia* is unique among living cetaceans. The teeth in the anterior region of the jaws, where the prey is typically first seized, are well suited to a grasping and holding function, while the molariform rear teeth are admirably adapted for mastication. The characteristics of these teeth suggest that *Inia* is specialized for feeding upon hard-bodied prey. When further information on

the natural foods of this dolphin becomes available, it may be found to feed extensively on armored or heavily-scaled fishes, such as certain of the South American catfishes, or perhaps even on mollusks or crustaceans of some kind. Our observation of a captive eating a gar shows that the dolphins are capable of taking hard-scaled prey.

In connection with their fluviatile habitus, there has been a general trend toward the development of bottom-feeding habits accompanied by reduced vision and greater reliance on the sense of touch among the living platanistids. Apparently the least specialized in this respect is *Pontoporia* which is the only form ranging into estuarine and coastal waters. The teeth of the La Plata dolphin are numerous, conical and slender, apparently specialized for grasping and holding relatively weak, soft-bodied prey. Its diet is reported to consist of cephalopods and various kinds of fish, including mullet and croaker-like species (Kcllogg, 1940; Cabrera & Yepes, 1940). *Lipotes* apparently feeds largely on fishes that it stirs out of the bottom muds with its elongate snout. Hoy (1923) obtained about two quarts of a species of eel-like, mud-dwelling catfish from the stomach of a specimen he collected. *Platanista* is the most highly specialized for bottom feeding of any of the platanistids. It apparently feeds almost exclusively by groveling in the bottom with the long snout. Since the eyes are degenerate, the Ganges dolphin probably locates its prey principally by touch (Anderson, 1878). The foods recorded for *Platanista* consist of several species of fish, including mud-frequenting species, and the crustacean *Palaemon carcinus*, which is also a benthic organism. In addition, such items as rice, seeds of other grasses, beetle remains, and an undigested bee have also been found in stomachs (Anderson, 1878). Such materials in all probability represent secondary or accidental ingestion. The present fragmentary data on the foods and feeding behavior of living platanistids, suggest that the feeding habits of *Inia* correspond most closely to those of *Lipotes*, with which it also shows closest taxonomic affinity. *Inia*, however, may be somewhat more pelagic in its feeding habits than *Lipotes*.

SEXUAL BEHAVIOR

The sexual behavior of the captive *Inia* appears to be essentially similar in kind and extent to that reported for captive delphinids (McBride & Hebb, 1948; Brown & Norris, 1956; Kritzler, 1952). The first instance of sexual activity was recorded after the dolphins had been in captivity about two weeks and involved masturbation by the small male. The incident was observed by

Warren Prince and Paul Cunningham. The dolphin had been swimming around in circles over a patch of white sand when an erection was noted. The penis in the fully turgid condition was dark in color, pencil-shaped and slightly curved anteriorly. Its length was estimated as between 10 and 12 inches. About the time the erection was noted the animal rolled over and began to swim on its back. It then proceeded to manipulate the penis with both flippers, at the same time bending the head forward to observe its actions. Ejaculation was not observed.

Numerous additional instances of sexual activity were observed after this date, and the frequency of this behavior increased during the late summer. Both dolphins were often seen swimming with erections, and occasionally one would attempt intromission with the other. On one occasion, the large male was observed to settle onto a large tin can sitting on the bottom and then perform thrusting movements with its body. This was apparently another form of masturbation.

The frequency of sexual behavior declined markedly following the separation of the dolphins in the pen in the main spring.

PLAY

The *Inia* exhibited a variety of behavior that seems best considered under the category of "play." Play activity originated spontaneously, since the dolphins received no special training or encouragement in the development of play habits during the tenure of their captivity. Although some behavior that might be construed as play was observed within a few days after the animals had been brought to Silver Springs, the frequency and complexity of play behavior increased after they had been in captivity for several months. The small male was somewhat more active in its play and played more frequently than the large one. McBride & Hebb (1948) noted that partly grown *Tursiops* are more playful than adults.

After only two days in captivity the large male was seen to seize a small stick thrown into the water nearby and to take it below the surface before releasing it. Whether this incident should be regarded as actual play or merely as an interest in possible food is not known.

What seemed clearly to be play was first noted on March 31, when we saw the small male pick up a piece of fish, toss it about in his jaws, and then release it. Following this he picked up a piece of water-logged wood off the bottom and repeated the performance. As the wood slowly sank to the bottom after being released, the dolphin swam past it and deliberately rubbed it with

his neck. Similar "toying" behavior in which the animals picked up dead fish or other objects off the bottom was subsequently observed on many occasions.

The dolphins also played with objects found at the surface. When in the pen in the main spring, they would often swim up and pull down a clump of hyacinths. After swimming around near the bottom, either upright or on their backs, and chewing the plants at the rear of the jaws, the dolphins would sometimes release the hyacinths, allow them to float part way to the surface then catch them again with a deliberate movement of the beak. Once a dolphin was seen swimming on its back near the bottom with a clump of hyacinths clasped in the axil of the flipper.

Sticks were a favorite play object. The dolphins would often play with a stick so vigorously and persistently that it would frequently be worn down and broken up into a number of smaller pieces. The small pieces of water-logged sticks found in the stomach of the small male at autopsy had apparently been swallowed during such play. When sticks or other buoyant objects were released under water, the dolphins would often swim after the object as it rose toward the surface and catch it with the forward edge of the flukes, keeping it delicately balanced there as they swam about.

After the dolphins had been placed in the main spring, the small male was observed playing with sticks above water. He would swim to the surface with a stick held in his jaws, thrust the forepart of his body out of water and toss the stick 4 or 5 feet away with a sluggish swing of the head. He would then quickly swim to the place where the stick had landed and retrieve it. This performance was repeated several times in succession. He also carried the stick around between the flipper and the body and would occasionally stand vertically in the water and toy with a stick lying on the bottom.

On one occasion an inflated rubber beach ball was thrown into the pen. The dolphins showed great interest in it and would often swim up beneath it and poke at it with the beak. After the ball was broken the large male was seen playing with a piece of it under water. He would swim about tossing it around and catching it again with the jaws, and he later tucked it into the axil of the flipper and carried it for some time in that manner.

In addition to individual play, the dolphins often engaged in joint play activity. The type of joint play most commonly observed consisted of passing a stick back and forth. This was first seen one evening after the dolphins had been

in captivity about a month. One would seize the stick in its mouth and swim off with it. As he swam along he would let the stick go, and catch it between the flipper and body. He would then release it again and catch it on the edge of the flukes. When the stick would slip off the flukes the other individual would grab it and repeat the performance. Even after the dolphins were separated in the pen in the main spring, they continued such play by passing the stick back and forth through the meshes of the fence.

Several times the young dolphin was observed in an apparent attempt to entice the other to play. On one such occasion he would swim up behind the large male, touch the rear part of its body with his beak, and then swim rapidly away as if expecting pursuit. He would also approach the large male from the rear and swim rapidly and warily past him without making contact with the beak. After passing, the small male would often swim downstream a short distance and then swing into a cove where, partially hidden by vegetation, he would watch the large individual. When the latter came close, the small male would leave his hiding place and swim rapidly away.

The small male became tame enough to attempt to initiate play with human beings. This he would do by swimming up to a person in the water, clasp a hand tightly between the flipper and the body, and then attempt to tow the person along. This behavior did not appear until the animal had been in captivity about five months.

As noted in connection with feeding behavior, one of the captives was observed catching live fish, shaking, and releasing them, and on occasion fish or snakes that had apparently been killed by the dolphins were discovered in the enclosure. It is possible that such behavior might have represented play. Wyman (1863) and McBride & Hebb (1948) remark that both *Delphinapterus* and *Tursiops* often play with small fish in captivity, frequently catching them in the mouth and releasing them, and that sometimes the fish are injured in the process.

Lamb (1954) reports that wild *Inia* are said occasionally to come up beneath the boat of a lone fisherman and seize the paddle. Such behavior may fall within the category of play.

Observations on captive marine delphinoids of several genera, including *Tursiops*, *Delphinapterus*, *Globicephala*, *Lagenorhynchus* and *Delphinus* (Brown, 1960; Brown & Norris, 1956; Kritzler, 1949, 1952; McBride, 1940; McBride & Hebb, 1948; McBride & Kritzler, 1951; Townsend, 1914; Wyman, 1863), have revealed highly

developed play behavior in both the young and adults. Although species differences exist, the play patterns that have been described are similar. The captive *Inia* exhibited most of the kinds of play reported for marine odontocetes, and play appears to be an equally important activity for them. Such differences as are apparent seem to have a structural rather than a motivational basis. For example, *Inia* does not appear to indulge in throwing objects above water as much as *Tursiops*, nor is it able to attain such distance and accuracy as the latter when it does attempt this type of play. This difference is apparently due to the fact that *Inia* is a much slower swimmer and more awkward than *Tursiops*. Brown & Norris (1956) have noted such differences, which also appear to have a structural basis, in the play behavior of *Lagenorhynchus* and *Tursiops*.

VOCALIZATION

Charles Hooper, one of the persons accompanying the first flight of *Inia* to Florida, reported hearing the large male utter squealing notes during the flight.

Two attempts were made to record sounds of *Inia* with a hydrophone during the early period of their captivity. Unfortunately, the dolphins engaged in little vocal activity on these occasions, and only two sounds are discernible on the recordings obtained (Schevill & Watkins, 1962). These include a loud rasping sound resembling a "bronx cheer" and a faint, plaintive yelping sound with a fundamental frequency of about 500 cps. The first sound may be comparable to the class of phonations termed "rasping and grating sounds" by Wood (1953) and reported by him for captive *Tursiops* and by Kritzler (1952) for *Globicephala*. Similar sounds are given by several of the delphinids included in the recordings of cetacean voices presented by Schevill & Watkins (1962). The yelping note of *Inia* is much lower in pitch than the majority of the odontocete vocalizations contained in the Schevill & Watkins' recordings. It most closely resembles certain calls of the white whale, *Delphinapterus*, the frequencies of which extend down to about 700 cps.

After the dolphins had been in captivity for some months, two additional sounds were heard by observers swimming underwater near the animals. These were described by Ricou Browning and William B. Ray as a high-pitched squeal and a loud "pow, pow, pow" made by snapping the jaws together. The sounds were heard only on infrequent occasions, and the circumstances under which they were emitted were not recorded in sufficient detail to permit drawing any conclusions as to their functional significance.

Squealing vocalizations appear to be characteristic of many marine odontocetes, and the sound produced by closure of the jaws is clearly the same as the "jaw clap" recorded for *Tursiops* by numerous authors (McBride, 1940; McBride & Hebb, 1948; Tavolga & Essapian, 1957; Wood, 1953) and interpreted as a form of intimidation display.

As previously noted, the captives sometimes gave an explosive snort when at the surface for air. In some cases this seemed to be simply a sneeze but in others the sound was emitted under circumstances suggesting that it might be an expression of alarm, surprise, or anxiety and thus have a communicatory function. One observation that lends itself to such an interpretation involved the large male. He was visited on the second night in captivity, and shortly after the observers had taken a position on the bank of the channel the dolphin swam toward them and snorted three times in quick succession. On another occasion, when one of the *Inia* was at the surface for air, it gave the snort when a pipe stuck in the bottom nearby was moved. Lawrence & Schevill (1954) note that an old female *Tursiops* studied by them frequently gave explosive blows before she became tame. They suggest that the sound may have about the same meaning as the snort of a horse.

Little information is available concerning the sounds of other platanistids. The sighing sounds described for the Ganges dolphin are apparently the normal accompaniment of respiration. Hoy (1923) notes that a wounded *Lipotes* gave a ". . . subdued bellow, somewhat after the nature of the noise made by a buffalo calf." He also mentions that a roaring noise heard at night on Tung Ting Lake is also attributed to the white-flag dolphin by the Chinese. This might also be a respiratory sound.

RELATIONSHIPS BETWEEN THE PAIR

During the early period of their captivity, the two *Inia* usually remained close together. The small male almost invariably took the initiative in maintaining the association. In some cases the two individuals swam side by side, with parts of the body in contact. The possible relationship of this behavior to echelon-formation swimming has been discussed under Locomotion. Often the small male would trail more to the rear of the other and not in such intimate association (Pl. IV, Fig. 9). He would frequently caress the large male with his beak or flipper or brush against him with other parts of his body and sometimes cross from one side to the other over the caudal peduncle of his companion. If he fell behind, he would increase his pace in order to

catch up and resume his previous position. Rarely did the large male attempt to regain contact with the smaller when the two became separated. In turning, the large male would nudge the small one with the head and beak if the latter was abreast of him (Pl. IV, Fig. 10). If the small male was in his typical position slightly to the rear, he would start his turn as soon as the large one began his without waiting for actual contact.

When the large male stopped to rest on the bottom, the small individual would follow suit. The latter was usually restless, however, and would move back and forth or nudge the large male with his snout, flippers, or other parts of the body.

During the early period of their captivity behavior suggesting antagonism between the dolphins was observed on only one occasion. The incident occurred while the large male was exploring the fence at the upstream end of the channel. During the time the large male was digging at the base of the fence and thrusting his beak gently through the wires, the small individual persisted in bumping him and nibbling at his flukes as if attempting to initiate play. Several times the big male, apparently annoyed, turned and gave chase to the smaller individual. Each charge carried the dolphins about 20 feet downstream. Once the small male lay on his side and arched his body as if in anticipation of an attack when the large male rushed at him, but in no instance was actual body contact observed. Prior to each charge, the large male released several large bubbles from the blowhole, and at one time during the period of observation a stream of small bubbles was seen escaping from the blowhole of the smaller dolphin. It is possible that the release of air noted in these instances was associated with the production of whistling or squealing vocalizations, as reported in several marine dolphins (Kritzler, 1952).

Usually the dolphins did not interfere with each others' feeding, even at times when they were swimming in close association. Often one would seize a fish off the bottom, toss it about a bit, then release it, whereupon the fish would be grabbed by the other dolphin and swallowed. In only two instances was a struggle over a fish seen. In both cases the dolphins were swimming together and the large male reached over and seized a fish being carried by the smaller individual. The small male attempted to hang onto the fish, the dolphins pulling and twisting it between them. In one instance the adult wrested the entire fish from the small male, and in the other the fish broke in two and each animal swallowed the piece it had retained.

After about a month in captivity, the pair began to exhibit a somewhat lessened tendency to associate together. Although the small male still trailed the other for considerable periods, he now began to make more frequent independent excursions to other parts of the channel. From this time on agonistic behavior between the pair increased. By the fall of 1956 it became necessary to separate the animals in the enclosure in the main spring, as the large male was persistently harrassing the other by chasing and biting it. A frequent maneuver of the large male was to swim up behind the other dolphin, seize his flukes, and pull him downwards and backwards. Such attacks were frequently carried out just as the small male was rising to the surface to blow.

No change in the behavior of the large male was seen after the younger animal died, except, as noted earlier, that it did not cross into the other side of the enclosure for several days after the fence had been lowered.

Cooperative behavior has been described for a number of cetaceans in the wild or under captive conditions (Hubbs, 1953; Siebenaler & Caldwell, 1956; Brown & Norris, 1956; Norris & Prescott, 1961). The degree to which this type of behavior is developed in *Inia* is unknown. Lamb (1954) recounts an instance of a herd of *Inia* gathering around one of their members that had been shot at, and Layne (1958) observed what appeared to be a somewhat similar case. The reaction of the large dolphin to a dead individual was tested on the first day of its captivity. While the dolphin was exploring the upper reaches of the channel, the body of the small male that had just died was slipped into the stream. Several minutes later the large male discovered the carcass on the bottom and swam slowly towards it until about 10 feet away. He then stopped and appeared to examine the body carefully, finally turning and swimming away. He repeated this performance twice more, once approaching quite close to the dead animal and appearing actually to touch its body with his beak. He made no attempt to "assist" the dead specimen in any way. Field observations indicate that *Inia* are not highly social and do not ordinarily associate in the closely-knit groupings of marine dolphins such as *Tursiops* and *Globicephala* (Layne, 1958). This apparent lack of a relatively strong social organization in *Inia* may thus be associated with a lesser tendency toward cooperative behavior.

DISCUSSION

The structural primitiveness of the plataniids raises the question of the status of their behavioral capacities as compared to those of

more advanced odontocetes such as the delphinids. Although the bottle-nose dolphin, *Tursiops truncatus*, has been the subject of many studies and more is known about its behavior than about any other cetacean, information on the behavior of the numerous other members of the Delphinidae is scanty. The same is true of the Platanistidae, *Inia* being the only form for which even the broad outlines of behavior are presently known. Thus, while it is of interest to attempt to compare the behavioral development of these two groups in view of the differences in their apparent phylogenetic position, the limitations of the data are such that any conclusions reached must for the present be regarded as tentative.

Among the more conspicuous behavioral characteristics of *Tursiops* are an apparently high order of learning ability, great sensitivity and responsiveness to the environment, elaborate and persistent play activity in both young and old animals, a high level and great diversity of sexual behavior and well developed group-oriented behavior. Included in the last category are a tendency to associate together in schools, the establishment of individual "friendships" and several kinds of cooperative behavior involving food getting, defense against enemies and assistance to injured individuals of the same or other species. The general pattern of behavior typified by *Tursiops* seems to apply also to other delphinids that have been studied, although species differences clearly exist. In fact, the same trends, most of which have a social basis, may underlie to a varying degree the behavior of all cetaceans, reaching their greatest development in the smaller marine odontocetes and in the bottle-nose dolphin in particular.

In this paper we have attempted where possible to compare our observations on various aspects of the behavior of *Inia* with data available for *Tursiops* and the other small toothed whales that have been kept in captivity. In so doing we have been more impressed by the similarities, both general and particular, in the behavioral patterns of *Inia* and the other forms than by the differences.

Although the data are admittedly inadequate, *Inia* does not appear to be innately less capable of being tamed and learning certain simple tasks than delphinids and the white whale. Its ability to master more difficult tasks remains to be demonstrated, but it seems likely that its capabilities will be found to lie within the range of the marine forms. No evidence of possible "insightful" behavior comparable to that recorded for *Tursiops* (Caldwell, 1956; Brown & Norris, 1956) has yet been recorded in *Inia*, but this may

reflect the difference in the degree to which the two forms have been studied rather than the fact that *Inia* is incapable of such behavior.

As is true of delphinids, the Amazon dolphin is alert and quick to perceive and respond to changes in its surroundings. The tendency of the captives to show fear of strange inanimate objects and to avoid them for a period of time resembles the behavior of the bottle-nose, common, and striped dolphins (McBride & Hebb, 1948; Brown, 1960). This trait, however, is apparently not consistent within the Delphinidae, as Brown (1960) did not observe it in a captive pilot whale.

The captive *Inia* also displayed the same type of play and sexual behavior described for marine odontocetes, and they seemed to be equally motivated to indulge in such activities. Because of its structure, *Inia* is less adept at certain kinds of play than *Tursiops*. Structural differences also seem to be responsible for variations in play behavior between species within the Delphinidae (Brown & Norris, 1956).

Several of the group-oriented behavioral characteristics of the delphinids also exist in *Inia*. Wild Amazon dolphins tend to travel in schools and show some development of cooperative behavior. In the captives, the occurrence of joint play and sexual activity, their close association during the early period of captivity, and the possible occurrence of echelon-formation swimming behavior may also be offered as examples of social development. The data available for *Inia* and delphinids also appear to indicate some basic similarities in vocal and other sounds that may play a role in communication. Jaw clapping, snorting, squealing, rasping calls and fluke-slapping may be cited as specific examples. It is also possible that further studies of *Inia* may reveal additional similarities in sound patterns to those of delphinids.

On the other hand, there is evidence that suggests that the social behavior of *Inia* is less well developed than that of *Tursiops* and perhaps the Delphinidae generally. Its schooling tendencies seem to be weaker, and one gains the impression of a lower level of interaction, such as cooperative behavior, between individual *Inia* in the wild than in many delphinids. The lack of evidence for the development of a close "friendship" between the captives as has been reported for *Tursiops* may be a further indication of a lower level of sociality in *Inia*. Our observations also suggest that the Amazon dolphin may be less vocal, in the sense of both the amount and variety of phonations, than *Tursiops*, and this might also be interpreted as evidence of weaker social orientation. Such a conclusion, however,

must be considered highly tentative. As shown by the studies of Lilly & Miller (1961) on *Tursiops*, the conditions under which observations are made may have a decided influence on vocal behavior. Thus, perhaps under other conditions of captivity or with more animals involved, greater vocal activity might be shown by *Inia*. It is also possible that differences in vocal behavior among the Delphinidae may be as great as those which presently appear to exist between *Inia* and *Tursiops*. Wood (1953) found pronounced differences in the extent and variety of vocalization of captive *Tursiops* and *Stenella* which he suggested were correlated with ecological factors in the wild.

In summary, there appears to be no basis for concluding that, despite the primitive aspects of its anatomy, *Inia* occupies a lower behavioral level than the delphinoid whales. The fact that the platanistids appear to be phylogenetically older than the delphinoids and yet possess equivalent behavioral capacities suggests that there may have been strong selective pressure for a common basis of behavior early in the evolutionary history of the odontocetes.

SUMMARY

Observations were made on two Amazon dolphins, *Inia geoffrensis*, captured in the Amazon River near Leticia, Colombia, in early March, 1956, and kept at Silver Springs, Florida. A young male lived 12 months in captivity and an adult male 15 months. An autopsy of the former revealed pieces of water-logged wood in the stomach, congestion in the lungs and an extensive hemorrhage in the brain. The large adult apparently died from severe bronchial pneumonia. Flukes (*Hunterotrema caballeroi*) occurred in the lungs of the small male and trematode eggs were found in its brain. The roundworm *Anisakis insignis* was present in the stomachs of two other *Inia* collected in the vicinity of Leticia.

The heart rate recorded in the captives under different conditions averaged 60 and 96 per minute. Two rectal temperatures obtained were 97.4 and 96.9°F. Organ weights of the small male are given, the brain weight/body length index of this individual being 88. A single erythrocyte count from a sample of blood taken from the abdominal cavity of a specimen shortly after death was 3,671,000 per mm³.

In a small channel where they were initially kept, the dolphins generally swam idly about in one pool for a long interval, then made a leisurely excursion to another, often returning to the original pool in a short time. They were somewhat

more active when placed in a pen in the main stream. Evidence indicated that the animals became habituated to their surroundings and were reticent to leave them. Scratching on the bottom or on protruding objects was a commonly observed activity. The dolphins evidenced no well-marked diel activity cycle. In the channel, the dolphins apparently slept on the bottom for brief periods. An apparently sleeping individual observed in the pen in the main spring floated off the bottom, with the body forming an S-shaped curve and only the tail in contact with the substrate.

The normal swimming speed was between 1 and 2 m.p.h., and the maximum speed recorded was approximately 10 m.p.h. The reduced dorsal fin and large, flexible flippers appear to be correlated with the relatively slow swimming speed. The general mechanics of locomotion are typically cetacean. In slow swimming a slight lateral movement of the tail stock was noted on occasion. This component was more pronounced when the dolphins were turning. The head is very mobile, being moved more during slow swimming than fast. The dolphins frequently performed barrel-rolls while swimming or from a position of rest and often swam upside down. Observations also suggested the occurrence of echelon-formation swimming.

Inia typically surface to breathe in a horizontal position, although they roll in more typical dolphin fashion under some conditions. In normal surfacing, the blowhole remains open for approximately 2 seconds. The mechanics of the blowhole operation appear to be similar to those described for delphinids. Intervals between blows ranged from 18 to 130 seconds. The small male tended to respire more often than the adult. There seemed to be a tendency for the dolphins to alternate a series of short intervals between breaths with ones of longer duration, although the pattern was not clear-cut.

Although the eyes are small, vision in *Inia* seems to be normally developed. As in other cetaceans, hearing is exceptionally acute and is probably the chief source of information about the environment. Circumstantial evidence suggests the existence of active echolocation in this species. The long beak appears to have an important function as a tactile organ, and the numerous, bristle-like hairs present on the beak probably contribute to this function.

The captives were quick to react to changes in their environment and showed a strong inclination to avoid strange objects under water. Without special training, they learned to respond to a splash as a feeding signal in a few days and in

three months' time had become quite tame. The younger individual was more curious and tamer than the adult. It would take food directly from the hand and allow a person to ride on its back.

The stomach of a wild *Inia* contained mostly fish remains (Characinidae), although a seed, insect fragments, and a small amount of vegetation were also present. The captives were fed dead fish. On only one occasion was a captive seen to capture and eat a live fish (gar). The pair consumed about 20 to 35 pounds of food per day. Fish under a foot in length were preferred. The prey was typically grasped with the tips of the long jaws then passed to the rear and masticated thoroughly before being swallowed head first. The dentition of *Inia* is obviously specialized for its particular manner of feeding. The anterior teeth are suited for grasping and holding and the molariform posterior teeth for mastication. The nature of the rear teeth suggest that in the wild *Inia* may take hard-bodied prey. The behavior of the captives and the specialization of the beak for probing suggest that *Inia* often feeds on the bottom. In comparison with other platanistids, *Inia* appears to resemble *Lipotes* most closely in its general feeding habits.

The dolphins frequently indulged in sexual behavior. Sexual activities recorded included masturbation, swimming with erections, attempted intromissions with one another and attempted copulation with inanimate objects.

Both animals engaged in considerable play activity. Individual play consisted of toying with sticks, pieces of vegetation and dead fish. Sticks were sometimes thrown out of the water and retrieved. The most common joint play activity was the passing of sticks back and forth as the dolphins swam around. This continued even after the animals were separated by a fence, the sticks being passed from one animal to the other through the meshes of the fence. The young individual was observed on several occasions engaging in behavior that suggested he was attempting to entice the larger individual to chase him. After five months in captivity, the small male would approach a human in the water and try to initiate play by clasping the person's hand against its body with a flipper and attempting to swim off.

The large male uttered squealing notes during the flight from South America. Sounds heard by observers under water included high-pitched squeals and a sharp, loud percussive note accompanied by clapping of the jaws. Under some conditions, a loud snort, produced by forced exhalation, appeared to represent some sort of communication, perhaps an alarm or warning signal. Two types of vocalization were recorded with a hydrophone.

During the first month in captivity, the two dolphins remained in close association at all times, the smaller individual taking the initiative in maintaining contact. Only one aggressive act was observed during this period. After this time the pair stayed together less and agonistic behavior increased, the large male being the aggressor in all observed instances. By the fall of 1956 it became necessary to separate the two animals, as the large one almost continually harassed the smaller.

Comparison of the behavior of *Inia* with data available for the bottle-nose dolphin and other small marine odontocetes suggests a basic similarity in the behavioral capacities of these forms. The fact that the platanistids are structurally more primitive than the delphinoids may indicate a strong selective pressure for a common behavior pattern early in the evolutionary history of the odontocetes.

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EXPLANATION OF THE PLATES

PLATE I

- FIG. 1. Adult male *Inia*. Note poorly-developed dorsal fin, large flippers, elongate rostrum, and conspicuous melon. (Photograph by Bruce Mozert, Silver Springs, Florida).
- FIG. 2. Adult male and young male swimming together during early period of captivity. The position of the small male suggests the possibility that this activity represents echelon-formation swimming.

PLATE II

- FIG. 3. Young male leaving surface after breathing. (Photograph by Bruce Mozert, Silver Springs, Florida).
- FIG. 4. Adult male breathing. Note the way in which the large melon deflects water away from the open blowhole.

PLATE III

- FIG. 5. Adult and young male breathing in synchrony.
- FIG. 6. *Inia* seizing dead fish at surface.
- FIG. 7. Adult male masticating fish at rear of jaws before swallowing.

PLATE IV

- FIG. 8. Jaws of an old adult female, showing worn and broken teeth in anterior part where prey is usually grasped.
- FIG. 9. Young male trailing adult in channel.
- FIG. 10. Adult male and young male turning while swimming together. Note more prominent crest on the caudal peduncle of the adult.